

# Dynamics of White Shark Predation on Pinnipeds in California: Effects of Prey Abundance

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**To assess long-term temporal trends in White Shark (*Carcharodon carcharias*) predation, and examine the relationship between *C. carcharias* and pinnipeds, we examined a 17-year (1988–2004) data set of daily shark attack surveys from Southeast Farallon Island (SEFI), California. We modeled within-season and among-year variation in the number of observed shark attacks at SEFI. Within-season, daily probability of attack was affected by hours of effort, date, tide height, and pinniped abundance. The seasonal peak in shark predation did not vary inter-annually. Daily probability of attack was positively correlated with pinniped abundance and negatively correlated with tide height. After controlling for within-season effects, 51% of annual variation in the number of observed shark attacks was explained by an inverse function of the abundance of Northern Elephant Seals (*Mirounga angustirostris*). The addition of shark abundance to the model did not significantly increase the model's descriptive power. This suggests a functional response where predation by *C. carcharias* increased with abundance of *M. angustirostris*, but plateaued once a critical density of *M. angustirostris* were available, either due to limitations of prey handling or satiation. We detected no temporal trend in annual number of observed shark attacks. Therefore, *C. carcharias* depends on *M. angustirostris* as a critical food source and will increase or decrease predation rates depending upon current seal populations.**

**A**NIMAL populations within marine ecosystems are regulated by both “bottom up” (i.e., food availability) and “top-down” (i.e., predation; Boveng et al., 1998; Valkenberg et al., 2004; Croll et al., 2005) factors. The degree of “top-down” regulation can be related to variation in the rate of predation on a given population, while variation in predation rate can be explained by changes in the abundance of either prey or predators within a system (Mech, 1966; Balser et al., 1968; Beukers-Stewart and Jones, 2004). Predators respond to evolving predator–prey dynamics through multiple functions. Increases in numbers of predators can increase predation rates (Valkenberg et al., 2004), but a stable predator population consuming prey at a rate that is positively correlated with prey availability, in other words, responding to prey availability, has a similar effect (Jordan et al., 1967). Behavioral traits of both prey (i.e., group size; Hunt et al., 1998; Honer et al., 2005) and predators (i.e., preference or prey switching; Ainley and DeMaster, 1980; Boveng et al., 1998) also influence this relationship. In addition, environmental conditions play a role in predator–prey dynamics (Connell, 1970; Paine, 1974; Robles, 1987).

Despite the high public profile of White Sharks (*Carcharodon carcharias*), and recent concerns for their conservation (Henneman and Glazer, 1996; Baum et al., 2003), there are still major gaps in our ecological understanding of this apex predator. Specifically, the predator–prey relationship between *C. carcharias* and their pinniped prey is not well understood (but see Le Boeuf et al., 1982; Ainley et al., 1985; Pyle et al., 1996a). Recent remote sensing studies focusing on *C. carcharias* and Northern Elephant Seals (*Mirounga angustirostris*) highlight research tools that illuminate behaviors by both *C. carcharias* and *M. angustirostris*. Time-depth recorders placed on *M. angustirostris* revealed that this species has adapted a diving pattern to potentially avoid encounters with *C. carcharias* (Le Boeuf and Crocker, 1996). Similarly, remote sensing has allowed researchers to observe behavior of *C. carcharias* over long periods, where receivers can locate individually tagged sharks continuously over many weeks, isolating their behaviors, and revealing

potential hunting strategies (Klimley et al., 2001). As a result, we now know that sharks are equally active both day and night, hunt alone, and show no sign of being territorial (Goldman et al., 1996; Klimley and Anderson, 1996). Further, identification of individual sharks through photographs or video has allowed researchers to identify individuals, ascertain inter-annual longevity, and determine that both sexes are present at certain foraging sites (Klimley and Anderson, 1996; Anderson and Pyle, 2003).

Southeast Farallon Island (SEFI) provides an excellent model system of interactions between *C. carcharias* and pinnipeds. SEFI is in the California Current ecosystem and supports significant populations of *C. carcharias* as well as large populations of the California Sea Lion (*Zalophus californianus*) and *M. angustirostris* (Sydeman and Allen, 1999). Based on early standardized counts of pinnipeds on SEFI and incidental observations of *C. carcharias*, Ainley et al. (1981, 1985) suggested a positive correlation between abundance of *M. angustirostris* and annual evidence of attacks by *C. carcharias*. As immature *M. angustirostris* arrived at the island in autumn to molt and the seasonal population increased, the number of incidentally observed attacks by *C. carcharias* peaked correspondingly. Following three years of standardized observations from SEFI (1987–1989), Klimley et al. (1992) found a seasonal peak in predation events during October and November. However, they noted that attacks were not evenly distributed temporally within years, but occurred as bouts of activity followed by a hiatus. Pyle et al. (1996b) and Anderson et al. (1996), after five years of standardized observations at SEFI (1988–1992), found that annual attack numbers were influenced by the environmental factors of tide height, swell height, and water clarity. Attack probability appeared to be positively correlated with tide and swell height, and negatively correlated with water clarity.

The SEFI time series is the longest continuous standardized study of predation by *C. carcharias* on pinnipeds in the world. While several variables have been suggested to affect the number of observed shark predation events at SEFI, no previous analysis has determined the most parsimonious

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Submitted: 21 January 2008. Accepted: 21 December 2009. Associate Editor: S. E. Wise.

© 2010 by the American Society of Ichthyologists and Herpetologists DOI: 10.1643/CE-08-012

explanatory model of factors affecting the numbers of observed shark attacks. Herein we present a model-selection analysis of the factors affecting predation rates by *C. carcharias* on pinnipeds at SEFI within and among 17 years of standardized daily observations. Our model selection procedure controlled for daily differences in effort, the assumption being that more effort would result in higher probability of sighting an attack. We also included wind speed to control for diminished detectability of attacks due to rough seas. We examined the seasonality of attack frequency to test the hypothesis that the seasonal peak in attacks was either stable or shifted annually. We included tide and swell height to test the hypothesis that higher water levels inundating low-lying haulout sites of pinnipeds result in more prey in the water. High water and resulting increased numbers of prey in the water could either increase (via increased opportunity) or decrease (via prey saturation) attack probability. We also investigated the effect of prey abundance on attack probability, specifically which species abundance best explained attack probability and the nature of the functional response. Our index of shark abundance tested the hypothesis that shark abundance either changed annually or was stable among years.

## MATERIALS AND METHODS

**Data collection.**—This study was conducted from 1988 to 2004 on Southeast Farallon Island (SEFI, 37°42'N, 123°00'W), located approximately 40 km offshore from San Francisco. Every year between 1 September and 30 November, trained observers from PRBO Conservation Science (PRBO) conducted “shark-watch” during all daylight hours, weather permitting. Working in two-hour shifts, observers constantly scanned the waters surrounding SEFI from the top of the island’s highest peak (Lighthouse Hill, elevation 95 m), searching for any sign of a predatory event (hereafter referred to as “attacks”). Most observed attacks involving pinnipeds lasted greater than five minutes and were accompanied by blood or a slick on the water, a circling flock of gulls, and/or vigorous thrashing of a shark on the surface. Due to the highly visible nature of the attacks, particularly the associated blood slicks and flocks of birds, we are confident that we missed few attacks within 1.6 km of SEFI (Ainley et al., 1985; Klimley et al., 1992; Pyle et al., 1996b). When an attack was detected, observers recorded the time and determined location of attack by theodolite (Leica Geosystems Inc., GA). Distance to attacks was calculated with ArcView 3.2 (ESRI Inc., CA) from theodolite data. Observations were terminated if visibility was reduced to less than 1.6 km or if winds were greater than 12.4 m/sec (25 knots). To document prey availability, we surveyed pinniped populations weekly throughout the duration of the study using standardized methods (Sydeman and Allen, 1999). Wind speed and swell height were observed five times daily at SEFI, and tide height data were obtained from Golden Gate tide station (37°48.4'N, 122°27.9'W). In 1997, all shark activity ceased following the predation of an individual of *C. carcharias* by Killer Whales (*Orcinus orca*; Pyle et al., 1999) on 4 October; therefore, we excluded all data from shark watches after the date of this observed event.

From 1991 to 2002, individually identifiable sharks were counted within each year, providing an annual index of abundance of *C. carcharias* at SEFI. We video-taped from a 4–5 m skiff every possible observed attack and shark visit to a

floating decoy within 1.6 km of the island. We excluded 1997 from this time series because no sharks were identified that year (Pyle et al., 1999). Sharks were identified from videos based on notable scars or missing sections of fins. All video analysis was conducted by one observer (ACB). Not every video-taped shark was identifiable due to water clarity, video quality, or lack of distinguishing features.

**Data analysis.**—We first examined within-season variation in the daily number of observed attacks using GLM with a Poisson distribution for count data in STATA 8.0 (StataCorp LP, TX). The data consisted of all shark-watch days from 1988 to 2004. Our response variable was number of attacks detected during each day of shark watch (range = 0–5). Due to small sample size of days with number of attacks greater than two, we pooled all attacks greater than two making daily responses zero, one, two, and greater than or equal to three. We looked at both linear and curvi-linear relationships in the model. Independent variables in the full model were: hours of effort, hours of effort<sup>2</sup>, day (Julian), day<sup>2</sup>, average daily wind speed (observed at SEFI), maximum daily swell height (observed at SEFI), maximum tide height during shark-watch (observed tide at Golden Gate station time-adjusted for SEFI), total pinniped abundance, abundance of *M. angustirostris*, and abundance of *Z. californianus* (weekly pinniped census), year (categorical), year \* day, and year \* day<sup>2</sup> interactions. To determine whether the seasonality of shark attacks varied within years, we examined the significance of year \* day and year \* day<sup>2</sup> interactions. We conditioned year on 1988 and Julian day began on 1 September.

We used POISGOF in STATA to determine goodness of fit for the full model. To determine whether the seasonality of shark attacks varied among years, we examined the significance of year \* day and year \* day<sup>2</sup> interactions before continuing with model selection on main effects. We dropped all year \* day<sup>2</sup> and year \* day interactions from the full model as insignificant because the 95% confidence intervals of all interaction coefficients included zero (Burnham and Anderson, 2002). For selection of main effects, we used a model selection with Akaike Information Criterion (AIC) as the metric of model parsimony (Burnham and Anderson, 2002). To control for inter-annual variation while selecting the best model of daily attack probability, models always included categorical year effects.

After the best within-season model was determined, we next examined annual variation in number of attacks using the full data set (1988–2004) to test for temporal trends, and to determine the best prey abundance variable. Our initial model set for annual variation analysis included annual variation in number of observed shark attacks as each year categorical, year trend, with year as a continuous variable, year trend<sup>2</sup>, a constant, and as linear functions of maximum pinniped abundance, average pinniped abundance, average abundance of *M. angustirostris*, maximum abundance of *M. angustirostris*, average abundance of *Z. californianus*, and maximum abundance of *Z. californianus*.

Finally, once the best variable of prey abundance was determined, we used data from 1991 to 2002 (excluding 1997) to examine the role of predator abundance and test theoretical functional response curves (Holling, 1965; Taylor, 1984). Models in this set included a constant, shark abundance index, prey abundance, prey abundance<sup>2</sup>, prey abundance<sup>3</sup>, ln(preyn abundance), and 1/preyn abundance.

**Table 1.** Model Selection Results of Daily Variation in Observed Shark Attacks from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W) between 1 September and 30 November.  $n = 1223$  observations, pin = total pinniped abundance, Zal = total *Zalophus californianus* abundance, Mir = total *Mirounga angustirostris* abundance, effort = daily hours of observation.

| Model  | Deviance | k  | AICc   | $\Delta$ AICc | AICc Weight |
|--|----------|----|--------|---------------|-------------|
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + pin                       | 1163.94  | 21 | 2370.7 | 0             | 0.30        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + pin + tide                | 1163.06  | 22 | 2371.0 | 0.3           | 0.26        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + Zal                       | 1164.53  | 21 | 2371.8 | 1.2           | 0.17        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + Zal + Mir                 | 1163.83  | 22 | 2372.5 | 1.8           | 0.12        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup>                             | 1167.21  | 20 | 2375.1 | 4.5           | 0.03        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + tide                      | 1166.37  | 21 | 2375.5 | 4.9           | 0.03        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + Mir                       | 1166.48  | 21 | 2375.7 | 5.1           | 0.02        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + pin + tide + wind + swell | 1162.62  | 25 | 2376.3 | 5.7           | 0.02        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + swell                     | 1166.93  | 21 | 2376.6 | 6.0           | 0.02        |
| year + effort + effort <sup>2</sup> + date + date <sup>2</sup> + wind                      | 1166.96  | 21 | 2376.7 | 6.0           | 0.01        |
| year + effort + effort <sup>2</sup> + date   | 1195.54  | 19 | 2429.7 | 59.1          | 0           |
| year + effort + effort <sup>2</sup>  | 1215.19  | 18 | 2466.9 | 96.3          | 0           |
| year + effort  | 1220.18  | 17 | 2474.9 | 104.2         | 0           |
| year   | 1249.93  | 16 | 2532.3 | 161.6         | 0           |

This set of models constitutes competing hypotheses of predator abundance and prey abundance as the best explanation for annual variation in number of observed shark attacks. The constant model indicates no influence of either predator or prey abundance (null model). The shark index model indicates the influence of predator abundance.

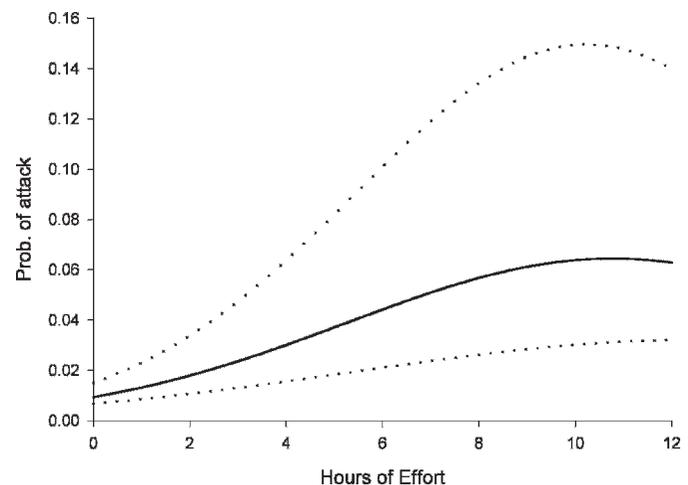
We examined competing models using model selection with AIC corrected for small sample size (AICc) as the metric of model parsimony (Burnham and Anderson, 2002). The most parsimonious model in the set is the minimum AICc model, with  $\Delta$ AICc = 0.  $\Delta$ AICc equals the difference between the AICc for a model and the AICc for the minimum AICc model in the set. The key to understanding model selection results lies within the AICc Weights column. AICc Weights are a measure of the strength of evidence that a given model is the best in the set. Due to model selection uncertainty, information from all models in the set when AICc Weight is greater than zero should be considered when making inferences (Burnham and Anderson, 2002). We used AICc Weights as importance values for covariates. Importance values are the sum of AICc Weights across all models that contain a given variable and indicate the descriptive power of that variable relative to the others in the set (Burnham and Anderson, 2002). The variable with the largest summed AICc Weight is estimated to be the most important, and the variable with the smallest summed AICc Weight is estimated to be the least important. When each variable is in the model set only once, AICc Weight equals importance. The ratio of AICc Weights between two models computes how many times better the numerator model is than the denominator model (Burnham and Anderson, 2002). The percentage of variation explained by covariate models was computed using analysis of deviance (ANODEV, Skalski et al., 1993).

## RESULTS

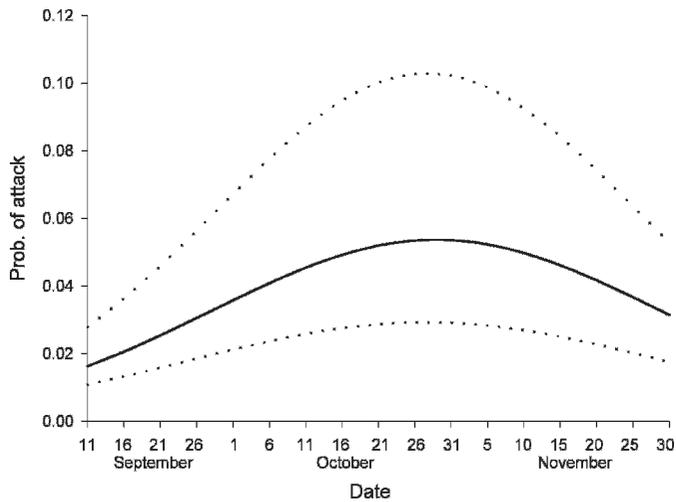
We completed 1,221 days of shark-watch at SEFI from 1988 to 2004. Shark-watch days with zero attacks had the highest frequency ( $n = 692$ ), followed by days with one attack ( $n = 369$ ), two attacks ( $n = 119$ ), and three or more attacks ( $n = 43$ ). Numbers of identified sharks per year ranged from 17–45 (mean  $\pm$  SE =  $35 \pm 9$ ). Poisson regression of temporal

variation in observed shark attacks with the full model indicated satisfactory goodness-of-fit ( $\chi^2 = 1097.29$ ,  $P = 0.909$ ).

Our AICc model selection results of daily variation in observed shark attacks included hours of effort, date, and total pinniped abundance in the top-ranked model (LR  $X^2_{21} = 210$ ,  $P < 0.001$ ; Table 1). The second-ranked model in this set included tide in addition to the above variables, and both of the two top-ranked models had nearly identical AICc Weights, indicating that either model could be the best. Effort (Fig. 1) and date (Fig. 2) were both quadratic functions (Table 2). Our mean peak attack date was 30 October. Date and date<sup>2</sup> had no significant interactions with year, suggesting the seasonal peak of shark predation did not change significantly over the 17-year study period. Weekly total pinniped abundance was positively linearly correlated with daily probability of attack, and maximum tide height during shark-watch was negatively correlated with daily probability of attack.



**Fig. 1.** Functional relationship (and 95% CI) between daily hours of effort on shark-watch and probability of observing an attack from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W) controlling for year, day, tide, and pinniped abundance.



**Fig. 2.** Functional relationship (and 95% CI) between Julian date (1 Sept = 1) and probability of observing an attack from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W) controlling for year, effort (daily hours of observation), tide, and pinniped abundance.

After controlling for daily variation due to effort, date, and weekly pinniped abundance, the variable “average abundance of *M. angustirostris*” was the most parsimonious model of annual variation in number of attacks observed (LR  $X^2_6 = 194$ ,  $P < 0.001$ ; Table 3). Abundance of *Mirounga angustirostris* explained 49% of the annual variation in number of attacks. We detected no temporal trend in annual number of observed attacks after controlling for significant within-year effects. Both variables for *M. angustirostris* were similarly ranked, and together these two models contained 98% of AICc Weight for this model set, indicating the clear superiority of *M. angustirostris* variables over others in the set.

After controlling for daily variation due to effort, date, weekly pinniped abundance, and an annual index of shark abundance, annual variation in observed shark attacks was best modeled as an inverse function of abundance of *M. angustirostris* for 1991 to 2002 (LR  $X^2_6 = 198$ ,  $P < 0.001$ ; Table 4, Fig. 3). The “inverse *M. angustirostris*” model explained 51% of the annual variation in number of attacks, and the “inverse *M. angustirostris* and sharks” model explained no additional variation. Model AICc Weights indicate that there is strong evidence for an inverse functional relationship between prey abundance and attack probability, whereas predator abundance was not an important factor affecting annual variation in shark attacks. The “inverse *M. angustirostris*” model was 2.7 times better

than the “inverse *M. angustirostris* and sharks” model, and the “sharks” model had zero AICc Weight. The “sharks” model alone explained only 5% of the annual variation in number of attacks.

## DISCUSSION

Our results indicate long-term stability in the seasonal peak of predation by *C. carcharias* at SEFI. However, annual variation in the number of attacks does exist and is correlated with the number of *M. angustirostris* present during the autumn haul out. Within each season, there was a quadratic relationship between date and probability of an observed attack (Fig. 2). The right truncated nature of this curve is due to shark-watches ending in early December. The inter-annual stability of the 30 October predation peak may indicate a fixed seasonality in shark movements to and from the Farallon Islands as part of larger movements by *C. carcharias* around the northeast Pacific. This conclusion is supported by the spatial stability of satellite tagged *C. carcharias* during autumn at the Farallones, in contrast to their long distance movements at other times of the year (Weng et al., 2007).

Several factors affected the within-season daily probability of observing a shark attack. The curvilinear diminishing return of increasing effort above nine hours per day on daily probability of observing an attack (Fig. 1) may suggest that the highest possible survey effort is not required to maximize observations of these rare events. However, effort cannot be distinguished from time of day, because shark-watches invariably begin in the morning, and the highest levels of effort are only attainable in the afternoon. Therefore, a more likely explanation is that probability of observing an attack is lower in late afternoon due to visibility issues, or behavior of predator or prey. Alternatively, the diminishing return of increasing watch effort beyond nine hours is that the period of daylight decreases during autumn resulting in reduced visibility during dawn and dusk at periods of ten and 11 hours, and hence it is harder to see attacks in the nearshore waters.

The negative relationship between tide height and the daily probability of observing an attack may be explained by the prey saturation hypothesis, where the predator must exert increased energy for consumption when prey levels become saturated and therefore decreases feeding activity during these periods (Abrams, 1990). As pinnipeds saturate the waters around the island, they are more likely to detect sharks through increased observation. Responses by sharks to tide height from this saturation of *Z. californianus* in the water at high tide likely cause *C. carcharias*, which tend to

**Table 2.** Model Coefficients and Statistics for Best Model of Within-Season Variation in Probability of Observing White Shark Attacks from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W) between 1 September and 30 November. Year-specific and constant coefficients excluded. Effort = daily hours of observation.

| Variable            | Coefficient | SE      | Z     | $P >  z $ | [95% CI] |          |
|---------------------|-------------|---------|-------|-----------|----------|----------|
| effort              | 0.3500      | 0.102   | 3.43  | 0.001     | 0.1500   | 0.5500   |
| effort <sup>2</sup> | −0.0162     | 0.0067  | −2.40 | 0.016     | −0.0294  | −0.00298 |
| date                | 0.063       | 0.0084  | 7.43  | <0.001    | 0.046    | 0.0790   |
| date <sup>2</sup>   | −0.0005     | 0.00008 | −6.59 | <0.001    | −0.00069 | −0.00037 |
| total pinnipeds     | 0.00014     | 0.00005 | 2.60  | 0.009     | 3.38E−05 | 0.00024  |
| tide                | −0.078      | 0.0585  | −1.33 | 0.183     | −0.193   | 0.0367   |

**Table 3.** Model Selection Results of Prey Abundance (*Mirounga angustirostris* and *Zalophus californianus*) Variables as Explanation for Observed Annual Variation in Shark Attacks from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W). All models included terms for effort, date, and weekly pinniped abundance to control for daily variation in observed shark attacks.  $n = 1223$  observations.

| Variable                               | Deviance | k  | AICc   | $\Delta$ AICc | AICc Weight |
|--|----------|----|--------|---------------|-------------|
| average <i>Mirounga angustirostris</i> | 1172.2   | 6  | 2356.4 | 0             | 0.53        |
| maximum <i>Mirounga angustirostris</i> | 1172.3   | 6  | 2356.7 | 0.30          | 0.45        |
| maximum <i>Zalophus californianus</i>  | 1175.9   | 6  | 2363.9 | 7.51          | 0.01        |
| maximum pinniped                       | 1176.4   | 6  | 2364.9 | 8.51          | 0.01        |
| constant                               | 1180.0   | 5  | 2370.1 | 13.66         | 0           |
| average <i>Zalophus californianus</i>  | 1178.6   | 6  | 2369.2 | 12.82         | 0           |
| average pinniped                       | 1179.7   | 6  | 2371.5 | 15.11         | 0           |
| year                                   | 1163.9   | 21 | 2370.7 | 14.27         | 0           |
| year trend                             | 1179.9   | 6  | 2371.9 | 15.53         | 0           |
| year <sup>2</sup> trend                | 1179.6   | 7  | 2373.2 | 16.84         | 0           |

attack by surprising lone individuals, to respond with decreased activity (Ainley et al., 1985; Long et al., 1996). Tide height results from this long-term study differ from those of Anderson et al. (1996); however, their results were very proximate in nature and seemed justified on the short term.

Our within-year data for pinniped abundance was too coarse to fit a specific daily functional response curve. However, assuming within-season shark population is controlled for by the day<sup>2</sup> seasonal curve, the positive linear relationship between weekly pinniped abundance and daily attack probability is evidence of some sort of within-season functional response.

Holling's type II functional response describes a non-linear reaction to increased prey levels. The simplest mechanism leading to a non-linear functional response is that predators need a certain amount of time to handle (kill, consume, and digest) their prey, where the functional response is linear when handling time is short but saturates if handling time is long (review in Jeschke et al., 2002). It is assumed that handling time is a genetically determined trait, where predators with long handling times, such as *C. carcharias*, are at a disadvantage because they can only capture a limited number of prey when prey is plentiful. At the same time, long handling allows predators to extract increased nutrients from an individual prey item, likely increasing the overall health of the predator (Abrams and Holt, 2002). Within the response, the predators are able to efficiently capture prey and regulate unsaturated prey levels. However, predators cannot regulate saturated prey levels,

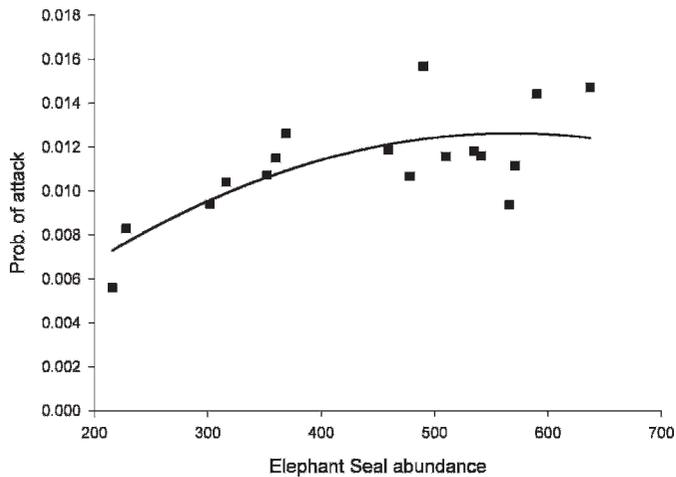
allowing high prey densities to grow unchecked, until predator density also increases. The prey cycles within this system show the importance of temporal variation in prey density (Abrams et al., 2003; Wilson and Abrams, 2005).

Our annual model results indicate a functional response of shark attacks increasing with abundance of *M. angustirostris* up to a plateau at the higher levels of prey density. Annual variability in number of predation events may not be a result of variation in shark abundance, rather than as a result of differences in abundance of *M. angustirostris* among years. This conclusion illuminates the importance of *M. angustirostris*, an energetically valuable prey type, as the driver of the number of predation events observed each year. A stable shark population that responds to increasing density of *M. angustirostris* with increased predation indicates *C. carcharias* may regulate this population of *M. angustirostris* from the top down. The implication of the shark's functional response to pinniped population densities on the marine ecosystem requires more investigation and tracking studies, such as those by Klimley et al. (2001), to provide insight into the reason for this leveling off of predation at high prey densities.

This study provides evidence that availability of *M. angustirostris* was correlated with number of observed attacks (Ainley et al., 1985; Klimley et al., 1992; Pyle et al., 1996a); however, the effect we detected was among years rather than within seasons. The positive relationship between observed predation events and abundance of *M. angustirostris* could also be due to differential detectability of prey species. Because carcasses of *M. angustirostris* float following

**Table 4.** Model Selection Results of Predator Abundance Index and Prey (*Mirounga angustirostris*) Functional Response Curves as Explanations for Observed Annual Variation in Shark Attacks from 1991–2002 on Southeast Farallon Island (37°42'N, 123°00'W). All models included terms for effort, date, and weekly pinniped abundance to control for daily variation in observed shark attacks.  $n = 822$  observations. sharks = shark population index.

| Model   | Deviance | k  | AICc   | $\Delta$ AICc | AICc Weight |
|---|----------|----|--------|---------------|-------------|
| inverse <i>Mirounga angustirostris</i>              | 801.71   | 6  | 1615.5 | 0             | 0.35        |
| log <i>Mirounga angustirostris</i>                  | 802.24   | 6  | 1616.6 | 1.06          | 0.21        |
| inverse <i>Mirounga angustirostris</i> + sharks     | 801.67   | 7  | 1617.5 | 1.94          | 0.13        |
| average <i>Mirounga angustirostris</i> <sup>3</sup> | 800.81   | 8  | 1617.8 | 2.27          | 0.11        |
| average <i>Mirounga angustirostris</i>              | 802.83   | 6  | 1617.8 | 2.24          | 0.11        |
| average <i>Mirounga angustirostris</i> <sup>2</sup> | 802.16   | 7  | 1618.5 | 2.92          | 0.08        |
| year  | 795.21   | 17 | 1625.2 | 9.65          | 0           |
| sharks  | 807.75   | 6  | 1627.6 | 12.08         | 0           |
| constant  | 808.38   | 5  | 1626.8 | 11.30         | 0           |



**Fig. 3.** Functional relationship between annual abundance of *Mirounga angustirostris* and the annual variation in shark attacks from 1988–2004 on Southeast Farallon Island (37°42'N, 123°00'W), controlling for daily variation due to effort (daily hours of observation), day, and weekly pinniped abundance.

the initial attack while *Z. californianus* sink (PRBO, unpubl. data), the detectability of events involving *M. angustirostris* may be higher, leading to an apparent difference in annual attack probability that is actually an artifact of our sampling methodology. Another caveat relates to the shark abundance index. Our finding that the shark abundance index explained very little annual variation in attacks could indicate a stable shark population, or that the index does not accurately reflect annual variation in shark abundance. Future efforts to gather reliable annual shark abundance data using echosounding should elucidate this factor (Klimley et al., 2001).

Our conclusions illustrate the importance of prey availability to the ecology of *C. carcharias*. While environmental factors and seasonality have been shown to have some effect on the timing of attacks, it is clear that overall pinniped populations, notably *M. angustirostris*, drive attack numbers at the Farallones. Further research into the population of *C. carcharias* and pinnipeds at SEFI is necessary to elucidate the relationship between *C. carcharias* and potential regulation of their pinniped prey.

#### ACKNOWLEDGMENTS

We thank all the biologists and interns who have painstakingly collected these data from the top of Southeast Farallon Island, most notably P. Pyle who was instrumental in the creation of this project as well as its development over the years. The support of the Farallon Patrol who regularly brought both supplies and staff to the island was invaluable. The staff of the Farallon National Wildlife Refuge, specifically J. Buffa, provided constant support towards our research and made life on the island incredibly enjoyable. We would also like to thank both W. Sydeman and M. Heithaus for reviewing earlier drafts of this manuscript. This is PRBO contribution 1578.

#### LITERATURE CITED

Abrams, P. A. 1990. Mixed responses to resource densities and their implications for character displacement. *Evolutionary Ecology* 4:93–102.

- Abrams, P. A., C. E. Brassil, and R. D. Holt. 2003. Dynamics and responses to mortality rates of competing predators undergoing predator–prey cycles. *Theoretical Population Biology* 64:163–176.
- Abrams, P. A., and R. D. Holt. 2002. The impact of consumer resource cycles on the coexistence of competing consumers. *Theoretical Population Biology* 62:281–295.
- Ainley, D. G., and D. P. DeMaster. 1980. Survival and mortality in a population of Adelie penguins. *Ecology* 61:522–530.
- Ainley, D. G., R. P. Henderson, H. R. Huber, R. J. Boekelheide, S. G. Allen, and T. L. McElroy. 1985. Dynamics of the white shark/pinniped interactions in the Gulf of the Farallons. *Southern California Academy of Science Memoirs* 9:109–122.
- Ainley, D. G., C. S. Strong, H. R. Huber, T. J. Lewis, and S. H. Morrel. 1981. Predation by sharks on pinnipeds at the Farallon Islands. *Fisheries Bulletin* 78:941–945.
- Anderson, S. D., A. P. Klimley, P. Pyle, and R. P. Henderson. 1996. Tidal height and white shark predation at the South Farallon Islands, California, p. 275–280. *In: The Ecology and Behavior of the White Shark*. A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Anderson, S. D., and P. Pyle. 2003. A temporal sex-specific occurrence pattern among white sharks at the South Farallon Islands, California. *Bulletin of the California Department of Fish and Game* 89:96–101.
- Balser, D. S., H. H. Dill, and H. K. Nelson. 1968. Effect of predator reduction on waterfowl nesting success. *Journal of Wildlife Management* 32:669–682.
- Baum, J. K., R. A. Myers, D. G. Kehler, B. Worm, S. J. Harley, and P. A. Doherty. 2003. Collapse and conservation of shark populations in the northwest Atlantic. *Science* 299:389–392.
- Beukers-Stewart, B. D., and G. P. Jones. 2004. The influence of prey abundance on the feeding ecology of two piscivorous species of coral reef fish. *Journal of Experimental Marine Biology and Ecology* 299:155–184.
- Boveng, P. L., L. M. Hiruki, M. K. Schwartz, and J. L. Bengtson. 1998. Population growth of Antarctic fur seals: limitations by a top predator, the leopard seal? *Ecology* 79:2863–2877.
- Burnham, K. P., and D. R. Anderson. 2002. *Model Selection and Multimodel Inference: A Practical Information-Theoretic Approach*. Springer, New York.
- Connell, J. H. 1970. A predator–prey system in the marine intertidal region. *Balanus glandula* and several predatory species of *Thais*. *Ecological Monographs* 40:49–78.
- Croll, D. A., B. Marinovic, S. Benson, F. P. Chavez, N. Black, R. Ternulla, and B. R. Tershy. 2005. From wind to whales trophic links in a coastal upwelling system. *Marine Ecology Progress Series* 289:117–130.
- Goldman, K. J., S. D. Anderson, J. E. McCosker, and A. P. Klimley. 1996. Temperature, swimming depth, and movements of a White Shark at the Southeast Farallon Islands, California, p. 111–120. *In: The Ecology and Behavior of the White Shark*. A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Heneman, B., and M. Glazer. 1996. More rare than dangerous: a case study of white shark conservation in California, p. 275–280. *In: The Ecology and Behavior of the White Shark*. A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.

- Holling, C. S.** 1965. The functional responses of predators to prey density and its role in mimicry and population regulation. *Memoirs of the Entomological Society of Canada* 45:1–60.
- Honer, O. P., B. Wachter, M. L. East, V. A. Runyoro, and H. Hofer.** 2005. The effects of prey abundance and foraging tactics on the population dynamics of a social, territorial carnivore, the spotted hyena. *Oikos* 108: 544–554.
- Hunt, G. L., Jr., R. W. Russel, K. O. Coyle, and T. Weingartner.** 1998. Comparative foraging ecology of planktivorous auklets in relation to ocean physics and prey availability. *Marine Ecology Progress Series* 167: 241–259.
- Jeschke, J. M., M. Kopp, and A. Tollrian.** 2002. Predator functional responses: discriminating between handling and digesting prey. *Ecological Monographs* 72:95–112.
- Jordan, P. A., P. C. Shelton, and D. L. Allen.** 1967. Numbers, turnover, and social structure of the Isle Royal wolf population. *American Zoologist* 7:233–252.
- Klimley, A. P., and S. D. Anderson.** 1996. Residency patterns of white sharks at the South Farallon Islands, California, p. 365–373. *In: The Ecology and Behavior of the White Shark.* A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Klimley, A. P., S. D. Anderson, P. Pyle, and R. P. Henderson.** 1992. Spatiotemporal patterns of white shark (*Carcharodon carcharias*) predation at the South Farallon Islands, California. *Copeia* 1992:680–690.
- Klimley, A. P., B. J. Le Boeuf, K. M. Cantara, J. E. Richert, S. F. Davis, and S. Van Sommeran.** 2001. Radio-acoustic positioning as a tool for studying site-specific behavior of the white shark and other large marine species. *Marine Biology* 138:429–446.
- Le Boeuf, B. J., and D. E. Crocker.** 1996. Diving behavior of elephant seals: implications for predator avoidance, p. 193–205. *In: The Ecology and Behavior of the White Shark.* A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Le Boeuf, B. J., M. Reidman, and R. S. Keys.** 1982. White shark predation on pinnipeds in California coastal waters. *Fisheries Bulletin* 80:891–895.
- Long, D. J., K. D. Hanni, P. Pyle, J. Roletto, R. E. Jones, and R. Bandar.** 1996. White shark predation on four pinnipeds species in central California waters: geographic and temporal patterns inferred from wounded carcasses, p. 275–280. *In: The Ecology and Behavior of the White Shark.* A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Mech, L. D.** 1966. The wolves of Isle Royal. *Fauna of the National Parks of the United States, Fauna Series* 7:1–210.
- Paine, R. T.** 1974. Intertidal community structure: experimental studies on the relationships between a dominant competitor and its principal predator. *Oecologia* 15: 93–120.
- Pyle, P., S. D. Anderson, and D. G. Ainley.** 1996a. Trends in white shark predation at the South Farallon Islands, 1968–1993, p. 275–280. *In: The Ecology and Behavior of the White Shark.* A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Pyle, P., S. D. Anderson, A. P. Klimley, and R. P. Henderson.** 1996b. Environmental factors affecting the occurrence and behavior of white sharks at the Farallon Islands, California, p. 275–280. *In: The Ecology and Behavior of the White Shark.* A. P. Klimley and D. G. Ainley (eds.). Academic Press, San Diego.
- Pyle, P., M. J. Schramm, C. Keiper, and S. D. Anderson.** 1999. Predation on a white shark (*Carcharodon carcharius*) by a killer whale (*Orcinus orca*) and a possible case of competitive displacement. *Marine Mammal Science* 15:563–568.
- Robles, C.** 1987. Predator foraging characteristics and prey population structure on a sheltered shore. *Ecology* 68: 1502–1514.
- Skalski, J. R., A. Hoffmann, and S. G. Smith.** 1993. Testing the significance of individual and cohort-level covariates in animal survival studies, p. 9–28. *In: Marked Individuals in the Study of Bird Populations.* J. D. Lebreton and P. M. North (eds.). Birkhäuser-Verlag, Basel, Switzerland.
- Sydeman, W. J., and S. G. Allen.** 1999. Pinniped population dynamics in central California: correlations with sea surface temperatures and upwelling indices. *Marine Mammal Science* 15:446–461.
- Taylor, R. J.** 1984. *Predation.* Chapman and Hall Ltd., London.
- Valkenberg, P., M. E. McNay, and B. W. Dale.** 2004. Calf mortality and population growth in the delta caribou herd after wolf control. *Wildlife Society Bulletin* 32:746–756.
- Weng, K. C., A. M. Boustany, P. Pyle, S. D. Anderson, A. Brown, and B. A. Block.** 2007. Migration and habitat of white sharks (*Carcharodon carcharias*) in the eastern Pacific Ocean. *Marine Biology* 152:877–894.
- Wilson, W. G., and P. A. Abrams.** 2005. Coexistence of cycling, dispersing consumer species: Armstrong and McGehee in space. *American Naturalist* 165:193–195.